Forest Health Protection

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Impacts of Stand Density on Lodgepole Pine and Lodgepole Pine Dwarf Mistletoe Spread and Intensification – and Comparison to Forest Vegetation Simulator (FVS) Projections:

A Long-term Study

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ABSTRACT

This study was established in 1971 to determine the impact of three thinning treatments on the spread and intensification of lodgepole pine dwarf mistletoe (LPPDM) in lodgepole pine (LPP). Thirty-eight years of field data were compared to Forest Vegetation Simulator (FVS) projections for the periods of 1971 through 2011 (40 years) and 1989 through 2009 (20 years) to determine how well FVS simulated LPPDM spread and intensification. As expected, thinning treatment spacing was positively correlated with LPP diameter growth. Thinning treatments showed no impact on the spread and intensification of LPPDM; however, trends appeared to be developing that may become more pronounced in future years. Initial infection levels significantly affected infection levels 38 years later. Low initial LPPDM plot ratings (dwarf mistletoe rating [DMR] ≤ 0.3 [average 0.1] on all 12 plots), and lack of LPPDM infected overstory proximate to the plots resulted in slow spread and intensification of LPPDM. After 38 years, plot DMRs ranged from 0.2 to 1.2 with an average DMR = 0.6. In comparison to field data, the 40 year FVS projections were fairly accurate at predicting spread of LPPDM in this study, but over-projected intensification about three-fold. FVS may require calibration for very light dwarf mistletoe infections (stand DMRs ≤ 1). Management implications of this study are discussed.

INTRODUCTION

Lodgepole pine dwarf mistletoe (LPPDM) (*Arceuthobium americanum* Nutt. Ex Engelm.) is present in more than one-fourth of the lodgepole pine (LPP) (*Pinus contorta* Douglas Ex Loudon) stands in Montana where it causes millions of cubic feet in lost volume each year (USDA 2006). In addition, LPPDM can cause deformed growth, early tree mortality, and changed fire behavior (Hawksworth and Johnson 1989, Shaw and Agne 2017).

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Dwarf mistletoe populations are polyetic, allowing for these parasitic plant populations to carry over and grow in successive seasons (Agrios 2005). Monocyclic polyetic tree disease populations, such as occurs with Dutch elm disease, have slow growth in early years of new populations before exponential growth causes rapid increase in damage (Fry 1982). The disease cycle for LPPDM is much longer – averaging about six years – causing the rate of dwarf mistletoe disease development in LPP to be extremely slow compared to other plant diseases (Hawksworth and Johnson 1989).

Although clearcutting has proven highly effective in reducing volume impacts caused by LPPDM (Dooling and Brown 1976), this treatment may be infeasible in areas where aesthetics, wildlife habitat, and other objectives must be met (Hawksworth and Johnson 1989). Long-term implications of intermediate treatments on spread and intensification of LPPDM must be understood to make sound forest management decisions in infested LPP forests.

This study was established in 1971 by Oscar Dooling to measure LPPDM spread and intensification in four precommercially thinned treatments (Dooling 1970 and Dooling et al. 1986) of LPP. Objectives were "to measure the impact, spread, and intensification of dwarf mistletoe on precommercially thinned…lodgepole pine in Montana" (Dooling et al. 1986).

Little is known about the effects of stand density on spread and intensification of LPPDM. Hoffman and Taylor (2008) described one study near Island Park, Idaho that investigated 8X8, 11X11, and 14X14 feet thinning treatments. Twenty years after thinning treatments, Hoffman and Taylor (2008) concluded there were greater infection rates on all thinning treatments compared to the non-thinned treatment. However, the infection rates of the non-thinned plots increased more than the thinned plots over the 20 year period. It should be noted that the infection rate of the non-thinned plots in the Hoffman and Taylor (2008) study was lower than the treatment plots when the study began, providing a great capacity for infection rates to increase. Results of the Hoffman and Taylor (2008) are inconclusive.

The Forest Vegetation Simulator (FVS) is a model used by silviculturists and other land managers to simulate forest growth and yield. These simulations can incorporate different forms of management and disturbance agents, including dwarf mistletoes (USDA Forest Service 2017). The Dwarf Mistletoe Impact Modeling (DMIM) System drives the dwarf mistletoe simulations within FVS. The DMIM users' guide (David 2005, pg. 10) states the model's spread and intensification module "is based on a study of 1,200 lodgepole pine in Gallatin National Forest in Montana (Dooling et al. 1986)." The featured 1,200 LPP were trees measured in an early phase of this study.

Analyses of this long-term LPPDM study will help land managers understand if thinning treatments have an effect on LPPDM spread, intensification, and subsequent impact on LPP. In addition, comparisons of field data with FVS simulations will help FVS programmers and end-users interpret simulations and identify areas within the base program and/or extensions that may require calibration.

METHODS

All LPPDM plots are located about one-quarter mile northwest of Hyalite Reservoir on the Gallatin National Forest. Potential vegetation for these plots is ABLA VASC (subalpine fir/grouse whortleberry) (Nosal 2017). Phase has been variously described as VASC (Nosal 2017) and CARU (bluejoint) (Berg 1974) and may perhaps be THOC (western meadowrue) (Pfister et al. 1977). Lodgepole pine age at study establishment was variable and estimated to be from one to approximately 22 years old (Berg 1974). Since trees were estimated to be up to 22 years old and the stand was dominated by early seral LPP in 1971, a stand replacing event likely occurred around 1950. Plots are located about 6,600 to 6,800 feet above sea level in elevation. The original project design included 36 plots (Figure 1).

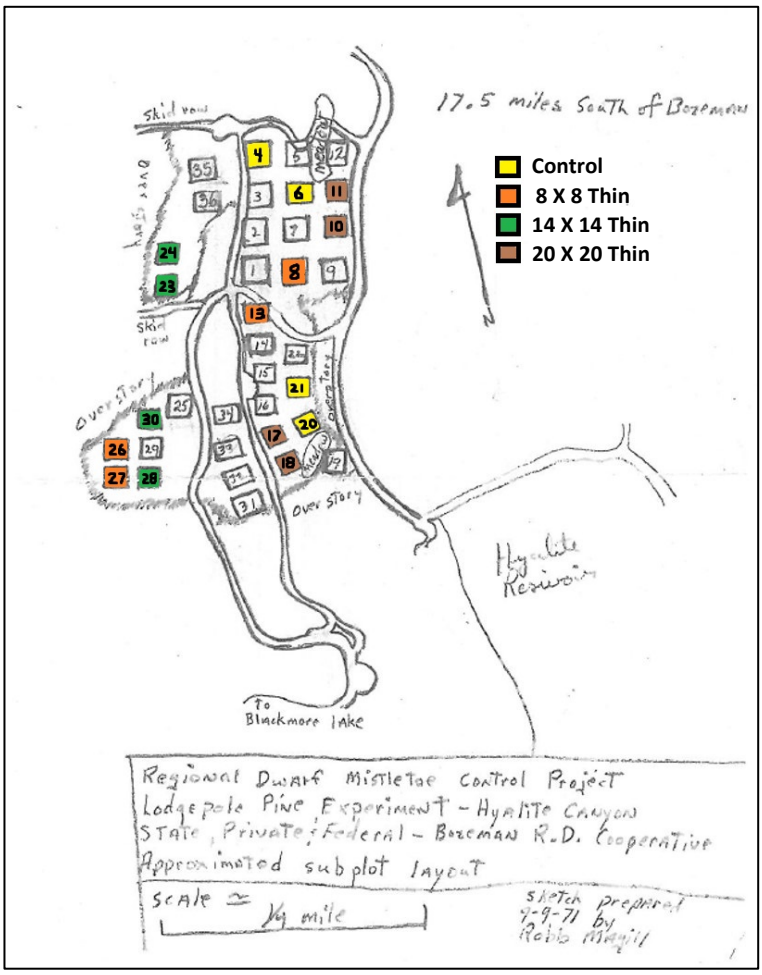

17.5 miles South of Bozeman
Control
8 X 8 Thin
14 X 14 Thin
20 X 20 Thin
Hyalite Reservoir
To Blackmore Lake
Regional Dwarf Mistletoe Control Project
Lodgepole Pine Experiment - Hyalite Canyon
State, Private, Federal - Bozeman R.D. Cooperative
Approximated subplot layout
scale ≃ ¼ mile
sketch prepared 7-9-71 by Robb Mayo

Figure 1. Original hand drawn map with colors added to show locations of plots measured in 2009.

Plots were established and thinned in 1971 and measured in 1971, 1974, 1979, 1984, 1989, and 2009. Original project design included three blocks (Table 1), with each block containing three half-acre square plots for each thinning treatment. Thinning treatments included a Control (no-thin), 8X8, 14X14, or 20X20 foot spacing. All trees were tagged in each plot, except the Control plots where 110 to 116 trees were tagged (data not shown). Tree selection protocol for Control plots is not clearly documented (Dooling 1970, Dooling et al. 1986); however, many trees in those plots were not tagged. In addition to stand-thinning treatments, sanitation through pruning and dwarf mistletoe removal were applied to some plots. For each thinning treatment within each block, one of three dwarf mistletoe removal treatments was assigned. These dwarf mistletoe removal treatments (pruning and/or removing trees with bole infections) were completed on some trees during plot establishment and through the 1979 measurement. From the 1984 measurement forward however, pruning was discontinued to "better define spread and intensification" (Dooling et al.1986). In order to eliminate this complicating factor, the mistletoe removal plots were eliminated from the data set for this analysis, other than plot 24 which had one tree pruned with no apparent effect on the following LPPDM measurement (Table 1).

Tree height, diameter at breast height (DBH), and crown length were measured on all tagged live trees at each measurement cycle. Tagged trees that were missing, dead, or damaged, were noted. In addition, dwarf mistletoe ratings for each crown third were collected as well as crown class (dominant, co-dominant, intermediate, suppressed). Dwarf mistletoe rating (DMR) was determined for each tree and

Table 1. Summary used to determine which plots were measured and analyzed; and, percentage of initial tagged trees that were lodgepole pine, subalpine fir and Engelmann spruce in each plot.

Plot No.	Block No.	Thinning Treatment	LPPDM Removal[1]	No. Inf. in 1989[2]	Measured in 1989[3]	Analyzed Here[4]	% LPP/SAF/ES in 1971[5]
1	I	14X14	None	0			-
2	I	14X14	None	0			-
3	I	14X14	None	0			-
4	I	Control	None	6	X	X	63/24/13
5	I	Control	None	4			-
6	I	Control	None	34	X	X	92/6/2
7	I	8X8	None	2			-
8	I	8X8	None	56	X	X	60/37/3
9	I	8X8	None	6			-
10	I	20X20	None	26	X		86/14/0
11	I	20X20	None	10	X	X	76/20/0**
12	I	20X20	1	5			-
13	II	8X8	None	18	X	X	88/11/0
14	II	8X8	None	2			-
15	II	8X8	None	0			-
16	II	20X20	None	1			-
17	II	20X20	None	10	X	X	88/12/0
18	II	20X20	None	9	X	X	80/20/0
19	II	Control	None	1			-
20	II	Control	7	7	X		74/21/5
21	II	Control	None	9	X	X	73/25/1
22	II	14X14	None	0			-
23	II	14X14	16	44	X		76/19/5
24	II	14X14	1*	31	X	X	77/19/4
25	III	8X8	None	0			-
26	III	8X8	None	17	X	X	69/27/4
27	III	8X8	50	54	X		76/23/1
28	III	14X14	None	24	X	X	75/23/2
29	III	14X14	2	6			-
30	III	14X14	None	11	X	X	79/20/1
31	III	Control	3	3			-
32	III	Control	None	4			-
33	III	Control	None	0			-
34	III	20X20	None	0			-
35	III	20X20	None	0			-
36	III	20X20	None	2			-

[1]Number of trees in plot that were pruned through 1979 measurement. *Although Plot 24 had one tree pruned in 1974, there appeared to be no effect on the 1979 measurement (DMR increased from 2 to 3 between measurements).

[2]Number of tagged lodgepole pine infected on the plot in 1989. This number was tallied from paper field forms to determine which plots would be measured in 2009.

[3]X indicates all tree measurements were taken in 1989 for respective plot.

[4]X indicates plot was used to complete analyses for this report.

[5]Percent of tagged trees that were lodgepole pine/subalpine fir/Engelmann spruce. Dash (-) indicates percent not determined since data entry was only completed for plots measured in 2009. **Plot 11 contained 4% ponderosa pine.

average DMR across each plot was calculated along with dwarf mistletoe index (DMI). Plot DMR is the average DMR of all susceptible trees on a plot and DMI is the average DMR of only infected trees on a plot. DMR provides an overall description of LPPDM severity in the plot, whereas DMI is a more specific indicator of LPPDM intensification (Hawksworth et al. 2002). Hawksworth (1977) describes procedures for measuring DMR and DMI. Intensification is the increase of DMR within a tree with a maximum rating of 6. Spread is the movement of LPPDM from an infected tree to a non-infected tree and is indicated for each plot by increased percentage of infected LPP.

In 2009, only 16 of the plots were measured to avoid measuring plots with little to no dwarf mistletoe detected through 1989 and to maintain an equal number of plots per thinning treatment (Table 1). Eighteen plots had five or less infected trees in 1989 (9 with no infections). Two plots with 6 infections each in 1989 were removed from the 2009 measurement to maintain an even number of plots per treatment.

Twelve of the 16 plots were analyzed (Table 1). In order to exclude plots that had been pruned early in the study, an additional plot per treatment was removed (n=3). Since the 20X20 thinning treatment had no pruned plot, one of those plots was randomly selected for removal from the analyzed data set to equalize the replicates for all thinning treatments.

Additional data were collected in 2009 beyond those collected in previous years. Height of highest and lowest dwarf mistletoe infections were measured to monitor upward advancement of LPPDM. In order to evaluate regeneration, ingrowth, stand densities (trees per acre [TPA]), and surmise future species composition, five 1/100th acre circular subplots were established in each of the 12 plots. One subplot was placed at plot center and one subplot was centered 15 feet inside each plot corner on an axis connecting the corner to plot center. Tree species, height, DBH if tree height $\geq$ 4.5 feet, LPPDM DMR, and other damage agents were measured in each subplot.

Since mountain pine beetle (MPB) (*Dendroctonus ponderosae* Hopkins) was active in the plots during the 2009 measurement, all 12 plots were visited in late June 2013 to assess MPB-caused mortality that took place from 2008 through 2012. These data may help indicate if thinning treatment and/or dwarf mistletoe rating had an effect on subsequent mountain pine beetle mortality.

Tree lists collected in 1971 and 1989 from each of the 12 plots were modeled through FVS to compare modeled results with actual tree measurements taken in 2009. The dwarf mistletoe extension is part of the base code for all western variants, including the Eastern Montana (EM) variant used in these model runs (Dixon 2002). No keywords were used to alter dwarf mistletoe or any other factors, except for Plot 30 where no dwarf mistletoe was recorded in 1971. Lodgepole pine dwarf mistletoe was added to this plot in 1979 using the Suppose Interface which included the 'MISTPINF' keyword in the 'MIST' extension (David 2005).

Statistical Analyses

The original design was adequately rigorous; however, low or no LPPDM infection levels were observed on many plots through 1989. Low initial infection rates, along with exclusion of plots treated years after establishment, left only three replicates of each thinning treatment for analysis. Therefore, power of statistical analysis was limited. Despite these challenges, this study provides valuable information otherwise unavailable considering the long timeframe over which these data were collected.

From data collected on tree status (live, dead, dwarf mistletoe presence, and dwarf mistletoe rating) and tree size, four response variables were calculated for each plot in 1971 and 2009. These response variables include percent infected, stand DMR, DBH, and tree height. In addition, the differences between 1971 and 2009 values for each response variable were calculated and used as unique response

variables *(percent infected change, DMR change, DBH change, height change*). The percent of trees that died over the course of the study *(% dead*) was also calculated for each plot and used as a response variable. One-way analysis of variance (ANOVA) tests, with thinning treatment as an independent variable, were conducted for each of these response variables (SAS Institute, Inc., Cary, NC). Bartlett's Test for Homogeneity was used to test for differences in variance. All data were assumed to be normal and, due to the small sample size, an alpha level of $p = 0.10$ was used.

RESULTS

Species Composition Changes from 1971 through 2009

Species composition and tree density (trees per acre [TPA]) at study establishment in 1971 were estimated for all plots. Initial species composition of Control plots is poorly understood since many trees were not tagged in those plots. All plots were dominated by LPP followed by subalpine fir, and most plots had some Engelmann spruce (Table 1). The 8X8 foot plots averaged 547 TPA, 14X14 plots averaged 246 TPA, and 20X20 averaged 97 TPA in 1971. The Control plots may be reasonably assumed to have had a higher TPA than the 8X8 plots but the exact stand density is unknown. No additional plot density data were taken until subplots were installed in 2009.

In 2009, subplot densities of the Control treatment averaged 1,060 TPA, 8X8 averaged 733 TPA, 14X14 averaged 893 TPA, and 20X20 subplots averaged 1,080 TPA for trees greater than 1.0 inch DBH (Table 2). The higher densities in the 14X14 and 20X20 treatments are due to subalpine fir and Engelmann spruce ingrowth, while the highest density of LPP occurred in the 8 X 8 spacing. Species composition in the stands is transitioning toward fir and spruce in all plots with LPP dominating only in the 8X8 treatment in 2009 (Table 2). Subalpine fir and Engelmann spruce seedlings were abundant in the understory of all treatments and composed over 97% of all seedlings in all treatments (Table 3).

Table 2. Comparison of mean trees per acre (trees ≥1.0 inch DBH) across three treatments and Control plots as measured in 2009 subplots.

	LPP*	SAF	ES	WP	DF	Total
Control	427 (107)	380	247	7	0	1060
% of Stems	40% (25%)	36%	23%	1%	0%	100%
8 X 8	467 (260)	220	47	0	0	733
% of Stems	64% (56%)	30%	6%	0%	0%	100%
14 X 14	233 (80)	507	147	7	0	893
% of Stems	26% (34%)	57%	16%	1%	0%	100%
20 X 20	247 (20)	553	280	0	0	1080
% of Stems	23% (8%)	51%	26%	0%	0%	100%

* Values in parenthesis represent either mean number of mistletoe infected stems per acre or percent lodgepole pine infected.
LPP = lodgepole pine; SAF = subalpine fir, ES = Engelmann spruce; WP = five needle pine (either whitebark or limber); DF = Douglas-fir.

Table 3. Comparison of mean seedlings per acre (< 1.0 inch DBH) across the three treatments and control plots as measured in 2009 subplots.

	LPP	SAF	ES	WP	DF	Total
Control	6	2707	1740	80	40	4573
% of Stems	0.1%	59.2%	38.0	1.7%	0.9%	100%
8 X 8	20	2640	1366	27	0	4053
% of Stems	0.5%	65.1%	33.7%	0.7%	0.0%	100%
14 X 14	20	2546	826	26	0	3418
% of Stems	0.6%	74.5%	24.2%	0.8%	0.0%	100%
20 X 20	40	1960	1760	27	0	3787
% of Stems	1.1%	51.8%	46.5%	0.7%	0.0%	100%

Effects of Thinning Treatments on Tree Growth and Mortality

Actual average spacing for each treatment plot in 1971 was determined by the following equation:

$$\sqrt{\frac{43{,}560}{(Number\ of\ trees\ in\ plot\ X\ 2)}}$$

Spacing was generally slightly wider than intended, except for the 14X14 which was slightly more dense than intended. The 8X8 treatment averaged 8.9X8.9 foot spacing with a range of 8.5 feet to 9.5 feet. The 14X14 treatment averaged 13.3X13.3 foot spacing with a range of 13.0 to 13.5 feet, and the 20X20 treatment averaged 21.2X21.2 foot spacing with a range of 21.1 to 21.8 feet spacing between trees.

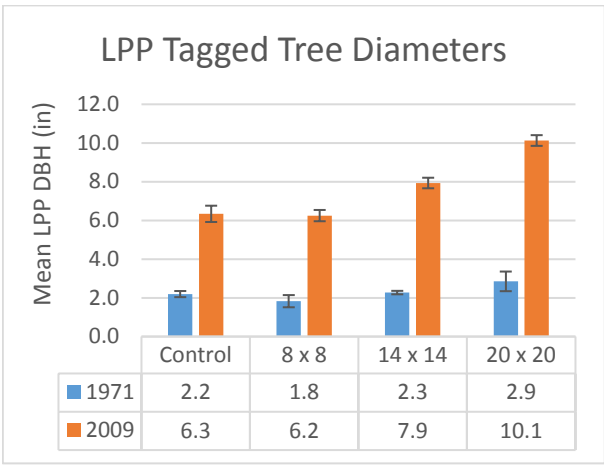


Figure 2. Mean plot diameters of lodgepole pine in Control and three thinning treatments in 1971 and 2009. Bars equal mean ±one standard deviation.

There were significant differences between treatments for the tree diameter response variable in the 1971 and 2009 standalone data, as well as the calculated difference between the two measurement years (Table 4). Mean 1971 LPP tree diameters were close to 2 inches in the Control, 8X8, and 14X14 treatments while the 20X20 treatment averaged closer to 3 inches (Figure 2). Differences in DBH among treatments were more pronounced in the 2009 data following a trend of increasing diameter with spacing greater than 8X8 feet (Figure 2). This result suggests that crop trees experienced growth release in the 14X14 and 20X20 treatments. Annual stem diameter growth was about 0.19, 0.15, 0.12, and 0.11 inches per year for the 20X20, 14X14, 8X8 treatments and Control, respectively over 38 years since treatment.

Differences in height were also significant, with notably shorter trees in the Control and 8X8 treatments as compared to the 14X14 and 20X20 treatments (Table 4, Figure 3). Lodgepole pine height growth averaged 9.6 feet across all treatments from 1979 to 1989. Over the following 20 years, decadal height growth was maintained at an average of 9.5 feet. Height growth was about one inch greater per year in the 14X14 and 20X20 treatments than the 8X8 treatment and the Control (data not shown) and was significant (Table 4).

Table 4. Analyses of thinning treatments effects on dependent variables over entire 38 year period of study.

Dependent Variable	df	*F*	*P*-value
DMR Change	3	0.66	0.59
1971 DMR	3	0.40	0.75
2009 DMR	3	0.27	0.84
% Infected Change	3	1.67	0.25
1971 % Infected	3	0.41	0.75
2009 % Infected	3	0.85	0.50
% Mortality	3	5.36	0.03
DBH Change	3	59.73	<0.0001
1971 DBH	3	5.52	0.02
2009 DBH	3	95.94	<0.0001
Height Change	3	3.39	0.07
1971 Height	3	6.87	0.01
2009 Height	3	10.90	0.003

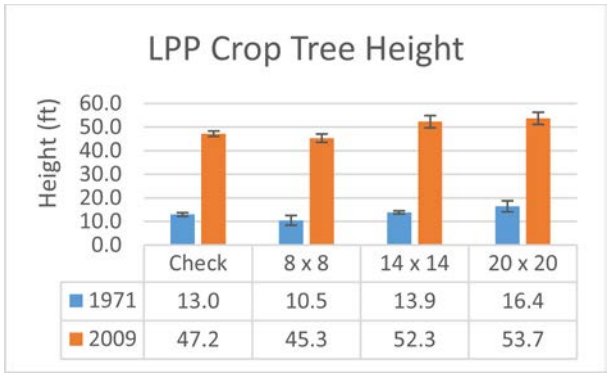


Figure 3. Comparisons of lodgepole pine crop tree height across treatments in 1971 and 2009. Error bars equal ± one standard deviation.

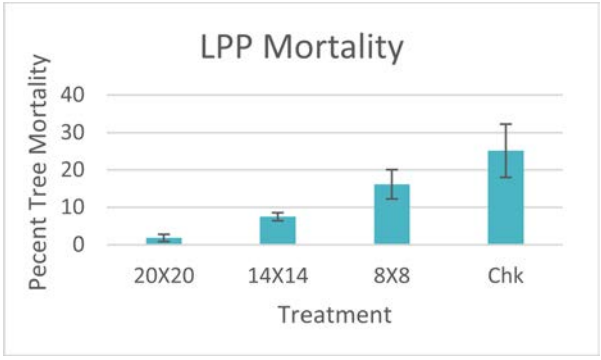


Figure 4. Comparison of the percentage of crop trees that died by any cause from 1971 to 2009. Bars equal mean ± one standard deviation.

Total tree mortality for the 38-year period was significantly higher in the more densely stocked Control and 8X8 treatments than the 14X14 and 20X20 treatments (Table 4, Figure 4). Most mortality occurred between the 1989 and 2009 measurements. Mortality was attributed by field crews to a wide number of agents including suppression, mountain pine beetle, secondary bark beetles, Christmas tree harvests, windthrow, snow damage, western gall rust (*Endocronartium harknessii* (Moore) Hirat.), animal feeding, heavy needlecast, suspected root disease, and LPPDM bole infections on two trees. Mountain pine beetle was the only mortality agent that appeared to be affected by thinning treatments.

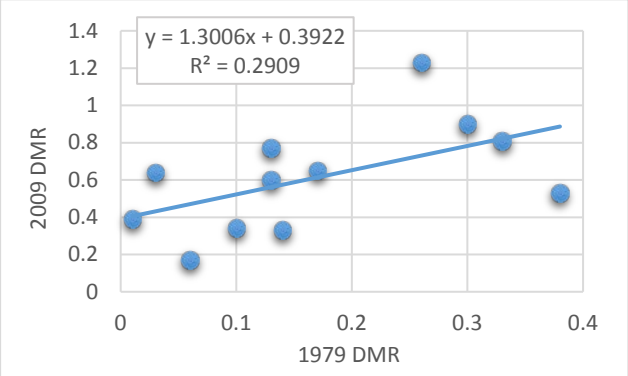


Figure 5. Scatter plot with fitted line comparing Stand DMR in 1979 and 2009.

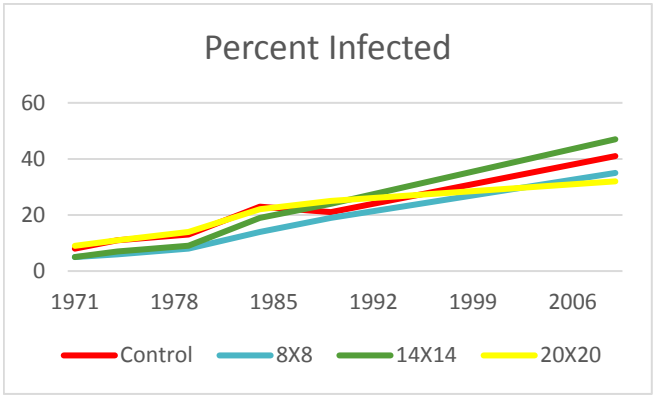


Figure 6. Percent of tagged lodgepole pine infected by dwarf mistletoe in Control and three thinning treatments over 38 years.

There were no statistical differences in LPPDM spread (percentage of trees infected) or intensification (mean stand DMR) among treatments over the 38-year study period (Tables 4 and 5). However, there were trends observed between the four treatments.

Stands with higher initial DMRs in 1971 generally ended with higher DMRs in 2009, regardless of treatment (Table 5). Plotting of the 2009 mean stand DMR for all plots against the 1971 mean stand DMR supported this observation (Figure 5). The significant R-square value of 0.29 suggests that nearly one-third of the change in DMR from 1971 to 2009 can be attributed to DMR in 1971.

Plot DMR is affected by both spread (percent infection) and intensification of dwarf mistletoe in previously infected trees (DMI). The smallest average increase in percent infections over 38 years was observed in the 8X8 and 20X20 treatments and the largest was the 14X14 treatment (Table 5, Figure 6). This partially explains the smallest increase in DMR over the study period occurring in the 20X20 treatment followed by the 8X8 treatment (Figure 7). In addition, DMI (average intensification across a plot) decreased in the 20X20 and the 8X8 treatments over the study period (Table 5, Figure 8).

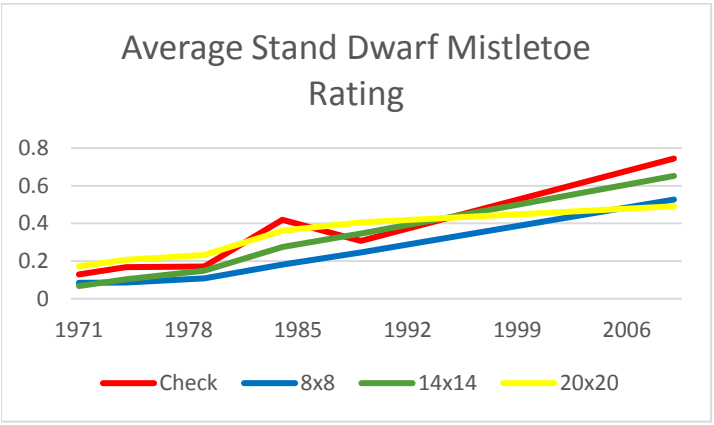


Figure 7. Change in average dwarf mistletoe rating (DMR) of lodgepole pine for Control and three thinning treatments over 38 years.

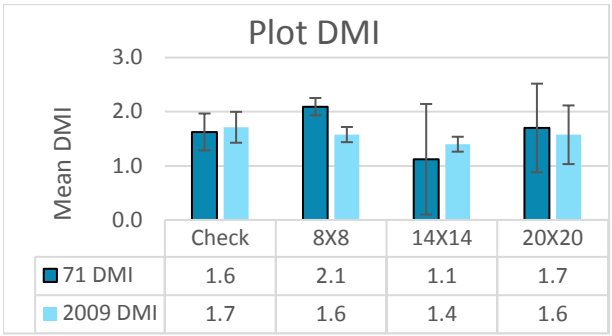
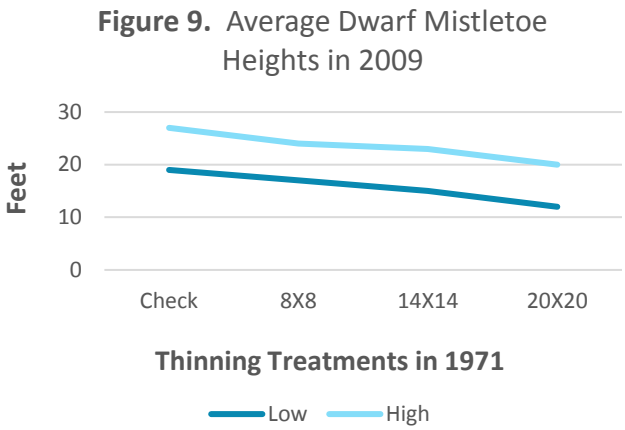


Figure 8. Comparisons of lodgepole pine dwarf mistletoe index (DMI) across treatments in 1971 and 2009. Error bars equal ± one standard deviation.



Upward movement of LPPDM was determined by measuring the lowest and highest infection on each tree in 2009. When averaged across all trees within a treatment, there was a direct trend of increased upward movement in the more densely stocked plots for both high and low dwarf mistletoe infections (Figure 9). The average low dwarf mistletoe height in each treatment was within 1.5 feet of the average crown height (bottom of crown) for the treatment and the average high dwarf mistletoe height was seven to eight feet above the average low dwarf mistletoe height for each treatment.

Table 5. Dwarf mistletoe rating, dwarf mistletoe index, and percentage of infected lodgepole pine trees in each plot for each measurement year.

Thin Trt.	Plot No.	1971				1974				1979			
		Live	%Inf	DMR	DMI	Live	%Inf	DMR	DMI	Live	%Inf	DMR	DMI
Control	4	71	6	0.1	2.0	71	10	0.2	2.0	70	10	0.1	1.3
Control	6	101	11	0.2	1.6	101	16	0.2	1.3	99	18	0.3	1.4
Control	21	83	7	0.1	1.3	83	7	0.1	1.2	83	10	0.1	1.0
Control	Average	85	8	0.1	1.6	85	8	0.2	1.5	84	13	0.2	1.2
8X8	8	144	18	0.3	2.3	143	15	0.3	1.8	142	18	0.3	1.6
8X8	13	235	2	0.0	2.0	232	2	0.0	1.6	228	4	0.1	1.8
8X8	26	210	2	0.0	2.0	205	1	0.0	1.7	205	2	0.0	1.5
8X8	Average	196	7	0.1	2.1	193	6	0.1	1.7	192	8	0.1	1.6
14X14	24	94	11	0.2	1.4	89	15	0.2	1.5	89	19	0.3	1.7
14X14	28	96	2	0.1	2.0	96	6	0.1	1.3	96	6	0.1	2.0
14X14	30	96	0	0.0	0.0	94	1	0.0	1.0	94	1	0.0	1.0
14X14	Average	95	4	0.1	1.1	93	7	0.1	1.3	93	9	0.1	1.6
20X20	11	35	4	0.2	1.5	35	9	0.1	1.7	35	11	0.2	1.5
20X20	17	43	1	0.0	1.0	43	7	0.1	1.7	43	7	0.1	2.0
20X20	18	39	5	0.3	2.6	39	18	0.4	2.0	39	23	0.4	1.7
20X20	Average	39	3	0.2	1.7	39	11	0.2	1.8	39	14	0.2	1.7
ALL	Average	104	6	0.1	1.6	103	8	0.1	1.6	102	11	0.2	1.5
Thin Trt.	Plot No.	1984				1989				2009			
		Live	%Inf	DMR	DMI	Live	%Inf	DMR	DMI	Live	%Inf	DMR	DMI
Control	4	68	12	0.2	1.3	67	12	0.1	1.0	47	30	0.6	1.9
Control	6	96	41	0.8	1.9	95	41	0.6	1.6	74	68	1.2	1.8
Control	21	82	16	0.2	1.4	80	11	0.2	1.4	73	25	0.3	1.4
Control	Average	82	23	0.4	1.5	81	21	0.3	1.3	65	41	0.7	1.7
8X8	8	141	33	0.5	1.5	139	40	0.6	1.5	119	51	0.9	1.7
8X8	13	222	6	0.1	1.4	221	8	0.2	1.8	178	11	0.2	1.5
8X8	26	204	4	0.1	1.3	201	8	0.1	1.3	183	42	0.6	1.5
8X8	Average	189	14	0.2	1.4	187	19	0.3	1.5	160	35	0.6	1.6
14X14	24	88	32	0.5	1.6	88	34	0.5	1.5	84	61	0.8	1.3
14X14	28	95	20	0.3	1.3	95	25	0.4	1.4	88	49	0.8	1.6
14X14	30	93	6	0.1	1.2	93	12	0.2	1.6	87	30	0.4	1.3
14X14	Average	92	19	0.3	1.4	92	24	0.4	1.5	86	47	0.7	1.4
20X20	11	35	23	0.4	1.9	35	29	0.5	1.7	34	29	0.7	2.2
20X20	17	43	14	0.2	1.7	43	23	0.4	1.5	42	26	0.3	1.3
20X20	18	39	28	0.4	1.6	39	23	0.4	1.7	38	42	0.5	1.3
20X20	Average	39	22	0.3	1.7	39	25	0.4	1.6	38	32	0.5	1.6
ALL	Average	101	20	0.3	1.5	100	22	0.4	1.5	87	39	0.6	1.6

Mountain Pine Beetle-caused Mortality

Nineteen LPP were killed by MPB from 2008 through 2012 (Table 6). The majority of trees killed by MPB were in the 14X14 and 20X20 thinning treatments.

Table 6. Mountain pine beetle-killed tagged trees from 2008 through 2012 compared to tagged lodgepole pine plot averages for DBH and DMR in 2009.

Thin Treatment	Dead to MPB (N)	Plot Avg. DBH	MPB-killed Avg. DBH	Plot Avg. DMR	MPB-killed Avg. DMR
Control	2	6.4 (1.2-10.8)	7.2 (6.4 & 8.0)	0.72	0
8X8	1	6.4 (0.6-11.6)	5.4	0.57	0
14X14	11	7.9 (0.9-13.9)	7.7 (5.3-11.1)	0.66	0.84
20X20	5	10.2 (4.4-14.2)	9.9 (8.7-11.0)	0.50	0.25
Avg. All Treatments	4.8	7.7 (0.6-14.2)	7.6 (5.3-11.1)	0.61	0.27

Comparisons of Field Collected Data to Forest Vegetation Simulator

Percent infected, DMR, and DMI were modeled in FVS for two cycles (20 years) using field data collected in 1989 and four cycles (40 years) from 1971. FVS projections were compared to plot data collected in 2009. FVS computations of 1971 DMR and DMI for each plot were identical to our computation in Excel spreadsheets in 22 of 24 instances (Tables 5 and 7). We were unable to determine the cause(s) of differences in Plot 6 DMI and Plot 8 DMR between FVS and our computations.

Lodgepole pine dwarf mistletoe infection percentages computed by FVS for 1971 were inconsistent with our Excel spreadsheet computations and increased more quickly than observed in the field (Tables 5 and 7). However, when averaged across all plots, LPPDM simulated infection percentages were similar to 2009 field data (Figure 6, Table 7). Both DMR and DMI were over-projected by FVS for all treatments (Tables 5 and 7, Figure 10). This can be interpreted as FVS providing a reasonably accurate forecast of spread, but an over-projection of intensification over the 40 year period (Table 7).

For the more direct measure of DMI, FVS projected an increase in all treatments and controls; however, there was a decrease in actual DMI in the 8X8 and 20X20 treatments in the field data (Table 7, Figure 8). Additionally, FVS projected an average DMI increase of 1.2 over 40 years across all treatments; whereas, field data showed DMI was stable across the 38 year study period.

Forest Vegetation Simulator projections substantially over-estimated DMR increase for each of the treatments (Figure 10). Trends for the 1971 and 1989 projections are very similar. The slopes for actual DMR increase are substantially less than both simulations, with the FVS 40 year projected DMR increase averaging about three times greater than actual 38 year DMR increase as determined through field collected data (Table 5, Table 7).

Figure 10. Forest Vegetation Simulator (FVS) projections of dwarf mistletoe ratings (DMRs) starting from 1971 (dark blue) and starting from 1989 (light blue) compared to field data (brown).

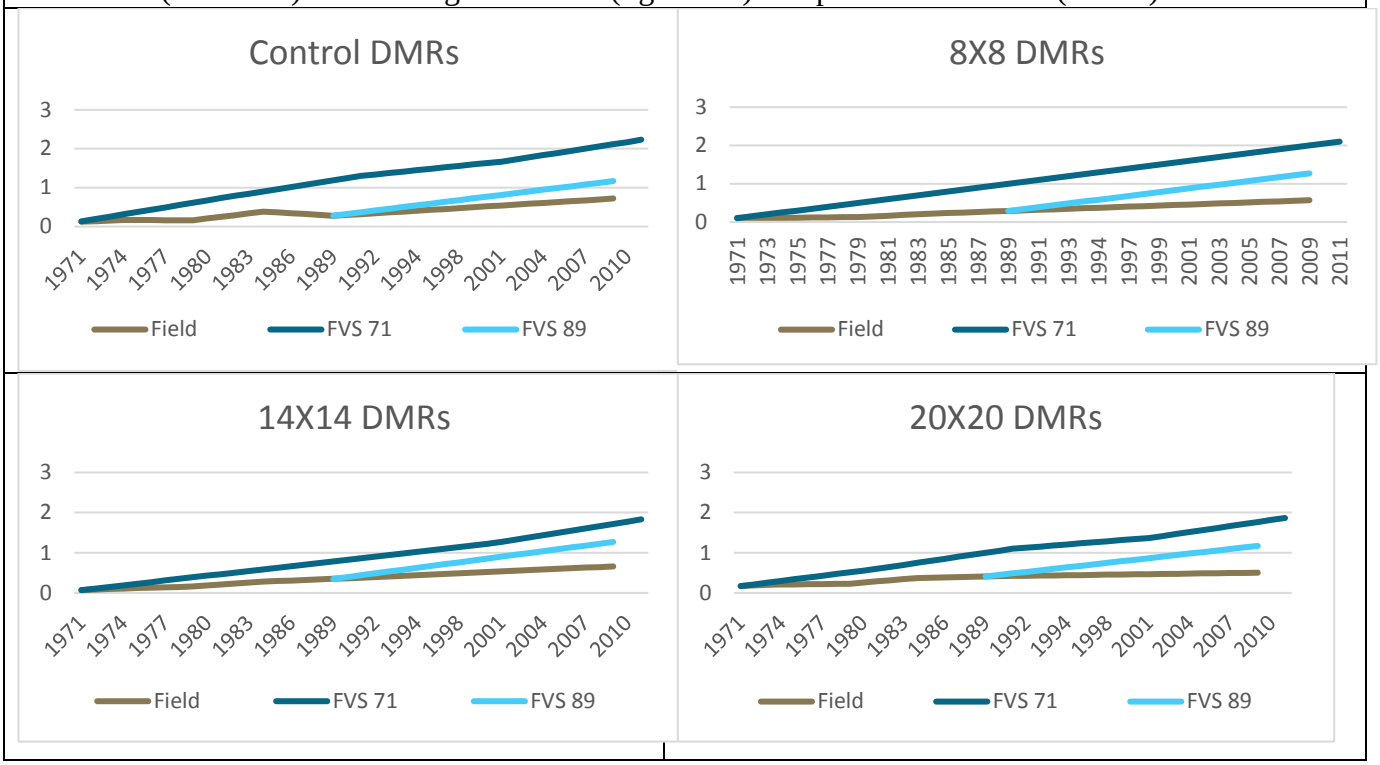


Table 7. FVS modeled dwarf mistletoe infection percent, DMRs, and DMIs in lodgepole pine.

Thin Trt.	Plot No.	1971			1981			1991			2001			2011		
		%Inf	DMR	DMI	%Inf	DMR	DMI	%Inf	DMR	DMI	%Inf	DMR	DMI	%Inf	DMR	DMI
Control	4	6	0.1	2.0	43	0.7	1.5	37	1.3	2.1	50	1.6	2.5	35	2.1	2.9
Control	6	11	0.2	1.5	50	0.9	1.6	48	1.5	2.2	68	1.9	2.5	48	2.6	3.0
Control	21	7	0.1	1.3	39	0.6	1.4	42	1.1	1.9	55	1.5	2.4	37	2.0	2.9
Control	Average	8	0.1	1.6	44	0.7	1.5	42	1.3	2.1	58	1.7	2.5	40	2.2	2.9
8X8	8	10	0.5	2.3	47	1.0	1.8	51	1.6	2.3	63	1.9	2.6	61	2.4	3.0
8X8	13	1	0.0	2.0	20	0.3	1.5	41	0.9	1.8	56	1.4	2.2	56	1.9	2.7
8X8	26	1	0.0	2.0	28	0.5	1.5	41	0.9	1.8	54	1.4	2.3	57	1.9	2.8
8X8	Average	4	0.2	2.1	32	0.6	1.6	44	1.1	2.0	58	1.6	2.4	58	2.1	2.8
14X14	24	12	0.2	1.4	51	0.9	1.7	49	1.5	2.2	66	1.9	2.6	41	2.5	3.1
14X14	28	2	0.1	2.0	30	0.5	1.5	34	0.9	1.9	52	1.2	2.1	41	1.8	2.6
14X14	30	0	0	0	1	0.0	1.0	14	0.2	1.2	34	0.7	1.6	29	1.2	2.2
14X14	Average	5	0.1	1.1	27	0.5	1.4	32	0.9	1.8	51	1.3	2.1	37	1.8	2.6
20X20	11	11	0.2	1.5	52	0.7	1.3	46	1.2	2.0	65	1.6	2.3	26	2.1	2.9
20X20	17	2	0.0	1.0	16	0.2	1.3	22	0.7	1.6	45	1.0	1.9	28	1.5	2.2
20X20	18	13	0.3	2.6	51	0.9	1.8	34	1.4	2.4	50	1.5	2.5	28	2.0	2.9
20X20	Average	9	0.2	1.7	40	0.6	1.5	34	1.1	2.0	53	1.4	2.2	27	1.9	2.7
ALL	Average	6	0.1	1.6	36	0.6	1.5	38	1.1	2.0	55	1.5	2.3	41	2.0	2.8

*No dwarf mistletoe detected in plot 30 in 1971. Dwarf mistletoe added in 1979.

DISCUSSION

Species Composition Changes from 1971 through 2009

Species composition can affect spread and intensification of LPPDM (Hawksworth and Johnson 1989). As stands age, subalpine fir and Engelmann spruce outcompete shade-intolerant LPP. Immunity and rare LPPDM infection probability in these two species, respectively, ensure that these species provide formidable barriers to the spread and intensification of LPPDM. Understanding the impact of fir and spruce ingrowth on spread and intensification is complicated due to infinite possibilities of tree sizes and distributions across a stand, but general species composition characterization may shed some light on the effects of increased amounts of these species in stands infected with LPPDM. After 38 years, the height of the great majority of spruce and fir are below the lowest dwarf mistletoe infections; therefore, are having only minimal or no impact on overall spread and intensification of LPPDM in the overstory. This may change in future years. Initial percentages of tagged trees on plots that were LPP ranged from 60 to 92% across plots in 1971 (data not shown). By 2009, LPP composition of all trees ≥ one inch DBH ranged from 23 to 64%. Multiple comparisons of species composition to LPPDM infection percentage, DMR and DMI showed no relationships. Perhaps a relationship will become evident after fir and spruce reach heights where they become barriers to LPPDM spread in the next one or two decades.

The greatest plurality of LPP occurred in the 8X8 thinning treatment (Table 2). This may be a relic of the original thinning treatments from which many more trees, including LPP, were retained in this treatment than the 14X14 and 20X20 thinning treatments. The Control treatment may have been too dense to allow LPP to compete with subalpine fir and Engelmann spruce. Once shade is cast by growing trees, potential for LPP ingrowth is greatly reduced and subalpine fir and Engelmann spruce will usually succeed in the absence of fire (Lotan and Critchfield 1990). Within this ABLA habitat series, it is not surprising that there is very little LPP regeneration compared to subalpine fir and Engelmann spruce (Table 3, Pfister et al. 1977). It is also no surprise that the additional sunlight initially available from the more open treatments, shows a consistent trend for more LPP regeneration, both in number and in species proportion than the more dense Control (Table 3).

Effects of Thinning Treatments on Tree Growth and Mortality

The larger 1971 diameters (Figure 2) and taller initial heights (Figure 3) in the 20X20 than the 14X14 and the 14X14 than the 8X8 treatments could be due to the retention of the most vigorously growing trees during thinning. Since more trees were selected for the denser treatments, smaller trees needed to be included to meet spacing requirements. Control treatment crop trees were similar in diameter and height to the 14X14 treatment. This is not surprising since the number of trees selected in the Control plots were similar to the 14X14 plots (Table 5), and many trees were left untagged in the Control plots. To provide additional support to this assertion, the diameters and heights of the 20 largest trees in each plot in 1971 were compared and found to be very similar in height and diameter with no apparent trends (data not shown). For these reasons, it seems reasonable to compare mean diameter increases to infer the effects of thinning on tree growth (Figure 11).

The direct effect of thinning is to reduce competition on retained trees (Lotan and Critchfield 1990). As expected, diameter growth was greater in the 20X20 than all other treatments; similarly, 14X14 was greater than the 8X8 and Control (Figure 11). Direct effects of thinning on LPP diameter growth is well studied and results of this study were generally consistent with previous investigators (Sullivan et al. 2006).

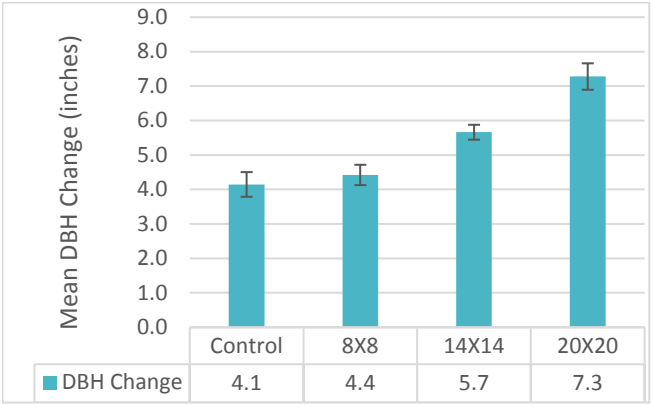


Figure 11. Mean increase in diameter at 4.5 above ground level (DBH) for three thinning treatments and Control.

Mortality caused by mountain pine beetle was greater in the wider spaced 14X14 and 20X20 treatments (Table 6); however, overall mortality from suppression, animal feeding, secondary bark beetles and other agents was much higher in the more densely stocked Control and 8X8 treatment (Figure 4). Given plot DMRs did not exceed 1.0 (Table 5) after 38 years, we cannot draw any conclusions regarding the interaction of thinning treatment effects on LPPDM spread and intensification with growth/mortality to this point. Perhaps a relationship will become evident after plot DMRs exceed 1.0 in the next one or two decades.

Effects of Thinning Treatments on Spread and Intensification of Lodgepole Pine Dwarf Mistletoe

It is commonly accepted that removing all residual infected LPP overstory after a stand replacing event would substantially reduce impacts from dwarf mistletoe over the subsequent generation (Hawksworth and Johnson 1989). The ages of trees in the study area suggests LPP within the plots are relatively even-aged. The slow spread and intensification of LPPDM in these plots suggests the overstory was removed early in stand development or did not exist when this stand was established. For dwarf mistletoe to have had a significant impact on LPP in these stands after 60 years (approximate age of stands), infected residuals with good distribution and coverage over the area would have needed to be retained for ten or more years after the stand replacing event.

The relatively consistent 7 to 8 foot wide zone of average dwarf mistletoe heights (Figure 9) across infections was unexpected. Since this zone moves up with increasing stand density (which tends to correspond with slight decreases in height), it would be reasonable to intuit that greater proportions of live crowns would be affected by LPPDM in denser stands. In turn, this relationship should correspond with substantially greater DMRs. However, more than half the trees remain uninfected, which suggests that initial DMR and initial percent infection appear to substantially influence DMR nearly four decades later. As infection levels continue to increase, differences may become more apparent between thinning treatments.

Spread of LPPDM through young stands has been described to be 1.5 times greater in open stands (no crown closure) than in closed canopy stands (Hawksworth 1958). Therefore, one may presume that LPPDM would spread more rapidly as spacing is increased by thinning treatments. Reviewing data in Table 2 of Hoffman and Taylor (2008), it appears that initial infection levels were important in determining infection levels 20 years after establishment of their study. They conclude that their Control treatment showed a greater increase in LPPDM infection than any of their thinning treatments. However, there was also a much greater capacity for increase in percent infection since the other treatments all had >50% infection rates at the beginning of their study. There appears to be no strong impact of thinning treatments on LPPDM spread and intensification in their study over the first twenty years. Likewise, results of this Montana long-term study do not readily support the assertion that LPPDM would spread

more rapidly as spacing is increased by thinning treatments. Rather, initial infection levels appear to be a more important factor in both the Idaho and Montana studies.

Lower DMR increase in the 20X20 treatments appeared to be a result of both spread and intensification of infected trees (DMI) lagging in this treatment compared to others. Even so, the difference was still statistically insignificant. Explanations for DMI decreases include a greater proportion of trees moving from DMR 0 to 1 (spread from tree to tree is faster than increase in DMR) of individual trees, tree height growth outpacing upward movement of LPPDM, or LPPDM plants dying due to the branch or entire tree they inhabit dying.

Even though thinning treatments in this study showed only limited, insignificant impact on the spread and intensification of LPPDM, an understanding of the distribution and intensity (DMR) of LPPDM within a stand can be used to affect our decisions on whether or not intermediate treatments will yield desired results. Current infection levels, distribution of those infections within a stand, and species composition seemed to provide good indications of future spread, intensification, and damage caused by LPPDM. Characterizing LPPDM in a stand can help land managers determine if intermediate treatments are beneficial or unnecessary with respect to dwarf mistletoe.

If limiting the impact of dwarf mistletoe on the current generation of LPP is a management objective, there are two feasible options. Thinning the stand to increase the growth rate of LPP so that it reaches merchantable size before LPPDM reaches a DMR of 4 or 5 where growth is substantially impacted is one option (Hawksworth and Johnson 1989). Another option which has proven effective involves removing infected overstory trees within the stand and adjacent (within 30 to 60 feet) to the stand before regenerating LPP is three feet tall or 10 years old (Hawksworth and Graham 1963). In most cases, LPP seed trees are unnecessary if cone-bearing tops are left in stands after harvest and therefore would not require additional stand entries if clearcutting is an option.

Spread and intensification in this study appears to be much slower than other LPPDM studies. Hawksworth and Hinds (1964) found that stands infected by LPPDM for 40 years in Colorado and Wyoming had an average plot DMR of 3.1, whereas this Montana study shows an average DMR of 0.6 after 38 years (92% of these plots were infested with LPPDM in 1971). Potential reasons for the differences include the fact that time since infection could only be estimated in the former study, and that some transects were adjacent to infected overstory trees. In this Montana study, we know infection levels throughout the study period and no infected overstory trees were within direct seed dispersal range of plots. Presence of overstory trees is essential in rapid establishment of LPPDM across a stand and is the reason for recommended removal of infected seed trees or adjacent infected stands before LPP regeneration is three feet tall or 10 years old when stands are primarily managed for wood production (Hawksworth and Johnson 1989).

Given the slow spread of LPPDM in the Montana study, there seems to be something different occurring compared to other studies of LPPDM. Perhaps the difference is the extremely low percent infection present at the beginning of the study in 1971. Hoffman and Taylor (2008) began their study in 1983 with 58% of their trees infected. Average plot infection for the Montana study at establishment in 1971 was only 6% with a range from 0 - 18% (Table 5). A similar study focusing on Douglas-fir dwarf mistletoe plots also started with very little dwarf mistletoe in all but one plot (Jackson 2008). The only plot that showed any substantial increase in DMR in that study was the plot that began with a DMR >1. Perhaps DMRs have a minimum threshold they need to meet before they increase at an accelerated rate. If that threshold exists, it may differ based on dwarf mistletoe species, host species, and trees species composition. Based on the limited data in Table 2 of Hoffman and Taylor (2008), it appears there may be a substantial acceleration in stand DMR at about 1.0 for pure stands of LPP. Since we had at least one plot in each thinning treatment and Control at a DMR of 0.7 to 1.2 in 2009 (Table 5), we may begin to see

an accelerated increase in DMRs beginning with the 2019 measurement if fir and spruce growth do not begin to impede spread of LPPDM.

Comparisons of Field Collected Data to Forest Vegetation Simulator

Since monocyclic polyetic plant pathogens may show slow growth for several years during early population development (Agrios 2005, Fry 1982), polyetic plant pathogens, such as LPPDM, which average six years per disease cycle may have an even more extended period of slow growth. Most LPPDM studies are conducted in stands with DMR≥1. Those studies begin when populations have already entered the exponential growth phase where DMR can be expected to increase at a rate of one every 10 to 15 years (Hawksworth and Johnson 1989). Hawksworth and Hinds (1964) noted that DMR increase was slowed in LPP stands under 14 years old and over 60 years old. Perhaps one explanation, or partial explanation, for this observation is that stands under 14 years old were still in the slow growth phase and over 60 years were in the deceleration phase of population development.

The over-projection of LPPDM DMR and DMI in FVS may be a result of FVS failing to distinguish between stands with an infected overstory within or adjacent to the stands and those stands with no dwarf mistletoe present in the surrounding overstory, particularly in stands with DMRs well below 1. This could be a substantial problem since dwarf mistletoe is automatically activated in FVS when tree lists contain any dwarf mistletoe (Dixon 2002). Based on results of this study as well as an associated study in very lightly infected Douglas-fir with no infected overstory (Jackson 2008), very lightly infected stands will show much more rapid intensification within a stand projected through FVS than will eventually play out in the field. Since spread of LPPDM seemed to be more accurately predicted by FVS than intensification in this study to date, perhaps FVS should focus on projecting spread until 50% of the population is infected before starting the exponential increase in DMR. Hawksworth (1977) suggested that after 50% of LPP is infected in a stand, stand DMR will equal about 1, and this appears to be supported in our study.

Another potential solution to this problem could be to grow LPPDM at a much slower rate when there is no overstory and infection levels <DMR 1. Continued monitoring and evaluation of the Idaho and Montana plots described above as well as PTIPS (Pest Trend Impact Plot System) plots should help to inform and further refine LPPDM simulations in FVS. However, it appears that only the Montana plots used as part of this study began with sufficiently low enough infection levels to better inform spread and intensification when DMRs are well below one.

Since LPPDM populations tend to grow much more quickly in young stands of LPP when within dwarf mistletoe seed dispersal range of infected overstory of the previous generation (seed trees, adjacent seed wall, etc.), the slow growth phase of LPPDM population cycle is greatly reduced if that infected overstory is retained in LPP for more than 10 years (Hawksworth and Johnson 1989). Therefore, FVS simulations may be more accurate for these stands than those stands with very little dwarf mistletoe infection when all infected overstory is removed. For these stands with very little dwarf mistletoe, LPPDM algorithms in FVS should be re-evaluated to better represent potential LPPDM population development.

Finally, it is difficult to understand how FVS's spread and intensification module is based on this current study (David 2005). FVS appears to dramatically overestimate intensification in its current state for the study in which the model is based.

Mountain Pine Beetle-caused Mortality

There were not enough trees killed by MPB to analyze statistically. It appears there were no preferences exhibited by MPB for LPPDM-infected or non-infected trees; however, a larger sample size would be necessary to have confidence in any trend.

MANAGEMENT IMPLICATIONS

There are two seemingly opposing ideas that can attempt to explain the impact of thinning on LPPDM spread. One, thinning may decrease LPPDM spread since a greater proportion of susceptible trees are infected when they are closer to infected source trees. In contrast, thinning may allow for more rapid spread since LPPDM seeds are not obstructed from flight – allowing infection to spread a further distance every disease cycle (Hawksworth and Johnson 1989). Over the 38 years since plot establishment, there were no significant differences between the thinning treatments; therefore, based on this study and other available information, practical thinning treatments do not have an appreciable effect on spread and intensification of LPPDM when dwarf mistletoe populations are at low levels.

However, research has shown that forest management practices such as sanitation thinning and/or pruning may reduce spread and intensification of LPPDM in young LPP stands (Alexander 1975, Brown 1978, Hawksworth, 1978, Hawksworth et al. 1987, Johnson 1999). Sanitation involves removing visibly infected branches or trees. Hawksworth et al. (1987) projected that cubic foot volume yields would be three times higher on sanitation-thinned plots than on untreated plots about 40 years after treatment. Sanitation during precommercial thinning may improve volume when less than 40% of the stand is infected (stand DMR well under 1) and all infected overstory is removed; and during commercial thinning when stand DMR is 3.0 or less and stocking is not reduced to unacceptable levels by removing infected trees (Hawksworth and Johnson 1989). Sanitation thinning did not provide acceptable results in western larch dwarf mistletoe (*A. laricis*) and Douglas-fir dwarf mistletoe (*A. douglassii*) infested stands in Montana (Merrill et al. 1988).

One could argue that these thinning treatments are irrelevant in the location of this study since trees will be lost to mountain pine beetle and/or overcome by subalpine fir and/or Engelmann spruce before differences in the thinning treatments/dwarf mistletoe interactions would have an appreciable effect on LPP health and volume. Without further treatment, fir and spruce will increasingly dominate all plots until a stand replacing event (wildfire or clearcut) takes place resulting in regeneration of LPP and possible sanitation of dwarf mistletoe.

The type of stand replacing event could have an impact on LPPDM. Muir (1993) found in her western Montana study that young LPP stands regenerated by fire were dominated more by LPP than clearcut stands, and that non-fire disturbance resulted in greater tree age variability. Clearcuts have been used for many decades as effective forest management tools to limit LPPDM (Dooling and Brown 1976). Broadcast burning after harvest may further reduce impacts by LPPDM in the subsequent generation.

The most effective manner to reduce impacts from LPPDM is not through intermediate treatments after dwarf mistletoe is well-established, but rather through sanitation of residual infected trees before regeneration is 3 feet tall or ten years old. If treatments are delayed, stands may be surveyed for dwarf mistletoe to determine if distribution and percent infection has surpassed the level when value from thinning will be realized. Surveys for accurate stand DMR measurements are best completed by walking through entire stands rather than using fixed radius plots due to the clumpy nature of dwarf mistletoe infections – this also helps determine the distribution of infections throughout a stand.

Results of this study suggest that stand DMRs increase much more slowly when stands are very lightly infected. Perhaps exponential growth may begin when DMR reaches a level around 1.0 as observed in western larch infected by *A. laricis* (Jackson et al. 2016). After that point in time, DMRs may increase incrementally in LPP about one every 10 to 14 years and growth impacts can be expected when DMRs reach 4 or 5 (Hawksworth and Johnson 1989).

CONCLUSION

After 38 years, this study has shown that LPPDM intensification was slower than anticipated in these very lightly infected plots with no infected overstory, and that initial plot infection levels influenced spread and intensification. Thinning treatments showed no impact on the spread and intensification of LPPDM; however, trends appeared to be developing that may become more pronounced in future years. Results showed that FVS projections for very low levels of LPPDM in this even-aged stand were overestimated and that the model should be calibrated for similar stands. Since several plots within this study are nearing DMR=1, future measurements may shed light on the point at which LPPDM populations move from slow to exponential growth. Therefore, continued measurement and analysis of these plots is recommended.

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